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The study of winter buds with reference to their growth and leaf content *

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(WITH PLATES 9–11)

The growth of buds in winter has been the subject of much speculation and discussion by the botanist and by the casual observer. This speculation and discussion, stimulated by an occasional winter of unusual mildness, has given rise to various theories about the disturbance of that quiescent state, or winter rest-period, which has stamped itself so indelibly on the trees and shrubs of our temperate zones. Inquiry into these theories, especially those relating to the winter growth of buds, discloses the fact that there has been comparatively little investigation or careful observation to substantiate them. The scattered statements which have crept into literature are, as a rule, merely opinions or passing observations made in the course of investigation of other phenomena.

Askenasy (1877) found some evidence of the growth of buds in winter. He says that the so-called period of rest, extending from about the first of November to the beginning of February, is one of extremely slow growth, a growth which in November becomes almost *nil.* His investigations, however, cover the rest period of but one species of our trees, *Prunus Avium,* the wild cherry, and include the study of the flower buds alone.

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From the investigations of Fischer (1891) and others, there is evidence that certain activities and various metabolic processes take place within the winter bud. Fischer claimed that to the external periodicity revealed in the phenomena of growth there is a corresponding internal periodicity in the processes of metabolism; that, in the buds and young shoots, movements and changes in the reserve material take place during the cool and cold seasons; and that these activities are dependent not only upon temperature but upon the inherent tendencies of the plant.

The results of Fischer's investigation would admirably supplement those of Askenasy had the latter considered a greater variety of plants. The study of flower buds of *Prunus Avium* alone can scarcely serve as a type for the growth of the leaf buds of all our trees and shrubs.

The problem of growth in the leaf bud during winter presents two important subjects for scientific research,—the question of growth, in so far as it relates to the enlargement of tissue through the addition of new cells or the stretching of cells already formed, and the question of leaf content dealing with the formation of additional leaf fundaments. These problems are considered in the present investigation.

METHODS

Material: As a basis for this study, observations and investigations have been made on the following twenty-two species, including seventeen different genera, of the common trees and shrubs of Wellesley, Massachusetts:

Fagus americana L. (American beech).
Fagus sylvatica L. (European beech).
Syringa vulgaris L. (lilac).
Ulmus americana L. (American elm).
Alnus incana Willd. (speckled alder).
Fraxinus americana L. (white ash).
Tilia vulgaris Hayne.
Tilia americana L. (basswood).
Acer platanoides L. (Norway maple).
Populus tremuloides Michx. (American aspen).
Betula populifolia Marsh. (American white birch).
Hicoria ovata Britton (shag-bark).

Hicoria microcarpa Britton (small-fruited hickory).
Salix fragilis L. (brittle willow).
Salix alba L. (white willow).
Aesculus Hippocastanum L. (horse-chestnut).
Quercus alba L. (white oak).
Quercus rubra L. (red oak).
Picea excelsa Link (Norway spruce).
Liriodendron Tulipifera L. (tulip-tree).
Rhododendron maximum L. (great laurel).
Philadelphus (mock orange).

DETERMINATION OF BUD CONTENT

For the study of leaf content, normal branches, upper and lower ones from various parts of the tree or shrub, were taken and studied during the months of November and December, 1905 and 1906. A long pruning shears was used to reach the upper branches. The number of nodes was counted and recorded for each season's growth, two and, where practicable, three years back. By this method a record of the number of leaves which were developed during those seasons was obtained. The terminal or upper axillary bud of each shoot, the nodes of which had been counted, was examined with a dissecting microscope, and the number of leaves found in the bud was noted.

FIELD OBSERVATIONS ON GROWTH

Observations on the growth of the bud were carried on during all of the winter and spring months. Ten normal buds of each genus were marked with a nurseryman's wooden label. During the latter half of November, 1905, and each month thereafter until the unfolding of the leaves in April or May, these buds were measured for the greatest length and the greatest diameter in each case. Measurements in length were made with a steel spacing dividers; measurements in diameter, with a micrometer screw caliper graduated to 0.01 mm. During the months of February, March, and April, measurements were made twice a month, once at the beginning and once at the close. Data resulting from these measurements, about 3000 in all, form the basis of the curves of growth as well as of the deductions on dormancy and growth in the gross study of buds.

MICROSCOPIC STUDY OF GROWTH

Collecting: Collections of material were made during the latter part of each month from November to April inclusive. Buds were cut from the high and low parts of each tree with the long pruning shears. The trees from which the buds were taken were situated in exposed and in sheltered places. In each case, however, the buds were cut from mature shrubs or trees and not from saplings or young growths.

Fixing: These methods are given in considerable detail because the varied character of the buds offered peculiar difficulties in fixing and cutting. In general, the bud scales were removed to the young leaves and the remainder of the bud was fixed entire. In the horse-chestnut the two outer whorls of leaves, and in the beech three lower leaves were also removed. Buds were placed directly in 20 per cent. alcohol and then passed successively through 40, 60, 80, 95 per cent. and absolute alcohol, remaining in each grade 24 hours. To insure perfect dehydration the absolute alcohol was changed once. The material was brought gradually into pure cedar oil by passing through the grades of alcohol and cedar oil, 33 and 66 per cent. cedar oil, 24 hours each. After remaining in cedar oil a few days, it was then carried through the grades of paraffin and cedar oil, 33 and 66 per cent. paraffin, to pure paraffin, melting point 54°, in which it was finally imbedded.

Staining: The buds were sectioned with a Minot-Zimmermann revolving microtome. In most cases they were cut 10μ in thickness. The exceptions to this were the woody and hairy buds, the hickory, oak, basswood, birch, and alder. These buds were cut from 25 to 50μ in thickness, depending upon the character of the bud. This greater thickness of the sections was not disadvantageous, since an outline study of the growing point, and not a cytological study, was desired. All sections were mounted serially. The usual method of staining with Delafield's hæmatoxylin was followed in all cases except one. The basswood sections are not well stained by this method because of the mucilaginous nature of the buds. The water used in the Delafield stain dissolves the mucilage which spreads over and obscures the tissue. A satisfactory stain was secured by using a solution of Bismarck brown in absolute alcohol. After the slides came from the xylol, they were stained horizontally two or three minutes and washed in absolute alcohol. They were then cleared and mounted in the usual manner.

GROSS STUDY OF BUDS

Leaf content: The observation that winter buds contain leaves is doubtless older than the science of botany. The final proposition to prove is, how many of the leaves which develop during the spring and summer actually exist in the bud at the beginning of winter. In a consideration of this question the number of leaves found in the terminal or upper axillary bud has been counted and compared with the number of nodes which developed in the same twig during the two or three preceding seasons. Such an enumeration, combined with a microscopical study of sections of buds fixed each month from November to May, 1905–6, and with field observations at the time of the unfolding of the leaves in the spring cannot fail to give results which must be regarded as conclusive.

Bailey (1898) says: "There are as many leaves packed away in the bud, as a rule, as there will be leaves on next year's shoot." He gives no citations of literature and presents no investigations on which to base this generalization. We are left in doubt whether an individual plant or different species of plants may show variation in this respect. All effort to find any published record more definite than this has been futile.

The whorls of leaves in the bud of *Acer platanoides* agree, as to number, with the number of nodes on the same twigs one, two, or three seasons back with the exception that, in some cases, the number of whorls is one more or one less than the number of nodes. Observations on a large number of primary branches together with the dissection of terminal buds show this variation in the number of nodes developed during different seasons. In fact, this tendency to variation is true of all trees and shrubs and is particularly noticeable in secondary branches. This discrepancy is easily explained by the fact that, practically under the same conditions, the number of nodes produced each season may vary slightly. Since the counts so nearly agree, it is, therefore, fair to assume that buds with four whorls of leaves will produce four nodes; those with three whorls will produce three nodes and so on. The number of nodes on the branches of each season is four or three. The number of leaves in the bud is six or four plus a pair of papillae in position for the fourth or third whorl of leaves.

A study of the microscopic sections of the bud during the winter and spring shows no organization of new leaves. At the time of the swelling of the buds in early April, new growths appear at the meristematic point (FIGURE 33, *s.f.*). Field studies during the period of the unfolding of the leaves show with perfect clearness that these new growths are the first pairs of scales of the future terminal bud, the bud of the next season. The new scales, admirably protected by the encircling bases of the petioles of leaves, show exceedingly slow growth in comparison with the normal leaves, and an unmistakable differentiation into bud coverings.

Bud dissection of *Aesculus Hippocastanum* shows that the full number of leaves exists in the bud at the beginning of winter. In addition two pairs of tiny scales appear as papillae in the meristematic point (FIGURE 36, *s.f.*). As they develop in the spring, the long, pointed character, indicative of scales, becomes prominent. The number of whorls of leaves in the bud of the main branches is generally four, sometimes five. This corresponds with the usual number of nodes developed in the branches during previous seasons. It is an interesting observation that the number of nodes is always less where the terminal bud is a flower bud.

Fagus americana and *Fagus sylvatica* have their leaves well developed in the bud and contain the full number for the season, five to seven on the primary shoots, three to four on the secondary ones. These leaves are, on the whole, farther advanced in regard to form and structure than those found on any other buds examined.

The number of leaves in the buds of *Fraxinus americana*, *Liriodendron Tulipifera*, and *Hicoria ovata* is more or less readily determined with the aid of the dissecting microscope, and agrees in each case with the usual number of nodes on the twigs of previous seasons — three or four whorls in *Fraxinus*, seven to nine leaves in *Liriodendron*, and five to seven leaves in *Hicoria*. A comparative study of the microscopic sections of buds during the winter months and the observations in the field during the unfolding of the buds gives undoubted evidence that here, too, the full number of leaves is packed away in the bud before the approach of winter.

Müller (1866–7) made an extensive study of *Fraxinus* from early spring to midsummer and found that the bud scales of the next season's terminal bud began a rapid development in April. The present study of *Fraxinus americana* confirms Müller's observations on this species, for, as will be seen by reference to FIGURES 34 and 35, no addition of leaves occurs during the winter months. The new additions, which take place after April 16, are the scales whose development has been traced by Müller.

Philadelphus enters upon the winter rest with the buds buried beneath the leaf scars. These buds were examined with difficulty, not only on account of their small size but because of the similarity between the outer coverings and the inner leaves. In the stained sections of the buds, these structures are differentiated and the leaves easily enumerated. Eight to ten whorls of true leaves are generally present and this is the usual number that unfolds. FIGURES 44 and 45 show median sections through a bud. The young whorls of leaves are closely appressed until the blades are quite well expanded. When the leaves are unfolded in May, there appear between the last two leaves two small, yellowish scale-like leaves which soon die away, evidently because the meristematic point itself ceases to function and thus terminates further growth at this point of the shoot.

There is little question that in the one conifer studied, *Picea excelsa,* the buds contain through the winter the complete number of rudimentary leaves. Küster (1899) says that in *Abies* and in *Pinus* the number of leaves in the bud is probably the same in the fall as during the time of unfolding. The present study would tend to confirm this view for *Picea,* since the earliest growth in the spring indicates a production of tiny scales at the growing point of the bud rather than the organization of more needle-like leaves.

The young leaves in the *Rhododendron* buds correspond frequently to the number of leaves and nodes present on shoots of the preceding season. The irregularity in branching renders the count difficult in growths of two successive seasons. The largest number of leaves counted in any bud is twelve; the largest number of nodes for previous years, fourteen. Because of the more or less whorled arrangement about the meristematic point, an exact enumeration of leaves and papillae is impossible from a study of serial sections. There remains, then, an element of doubt as to the number of leaves and leaf fundaments actually contained in these buds.

In buds of *Syringa vulgaris* the inner bud scales so gradually emerge into leaves that it is impossible to differentiate between them. In fact what appear to be *bona fide* scales in the bud develop into normal leaves as the buds unfold. These scars are crowded more or less into the ring of true scale scars which in part become obliterated by the growth of the stem. Any enumeration of nodes, therefore, in the shoot of the preceding season is untrustworthy as a criterion for the number of leaves contained in the winter bud. The microscopic sections are more satisfactory in that they admit of a detailed and minute study of the vegetative point. From these slides it is evident that the vegetative point exhibits a variation in ability to produce new leaves in addition to those already existing in the bud. It is believed, from a study of the slides, that buds, which early in the spring develop buds in the axils of the uppermost leaves, do not make new leaves at the apex of the growing point, but that buds in which these axillary growths are absent early in the growing season, continue to form new leaves (FIGURES 12 and 13). A probable explanation lies in the assumption that the energy of growth is directed to the upper axillary buds rather than to the meristematic point of the bud. These cells soon cease to function and die, thus terminating the growth of the stem. It appears, then, that the leaf content of the bud of *Syringa vulgaris* may receive additions in the spring. These new leaves are few, one or two pairs at the most. They never fully develop but shrivel away when the meristematic point ceases to function.

There is evidence that, in the leaf buds of *Salix fragilis* and *Salix alba*, the leaves are not all organized at the beginning of winter. The nodes on primary shoots vary from seven to thirty-six. The leaves found in any bud of these shoots do not exceed thirteen in number plus one or two papillae; moreover, the very nature of the growing end, with its continued production of closely appressed leaves, seems to establish the conclusion that the leaf content is not complete in *Salix* at the beginning of winter.

In the buds of *Populus tremuloides* the leaves, from five to nine in number, are very small but comparatively well formed. The number of nodes found on the growth of a given season varies from six to twelve. A growth of six nodes may follow one of six, ten, or twelve nodes and *vice versa*. This irregularity in the amount of growth occurs during different seasons or in the same

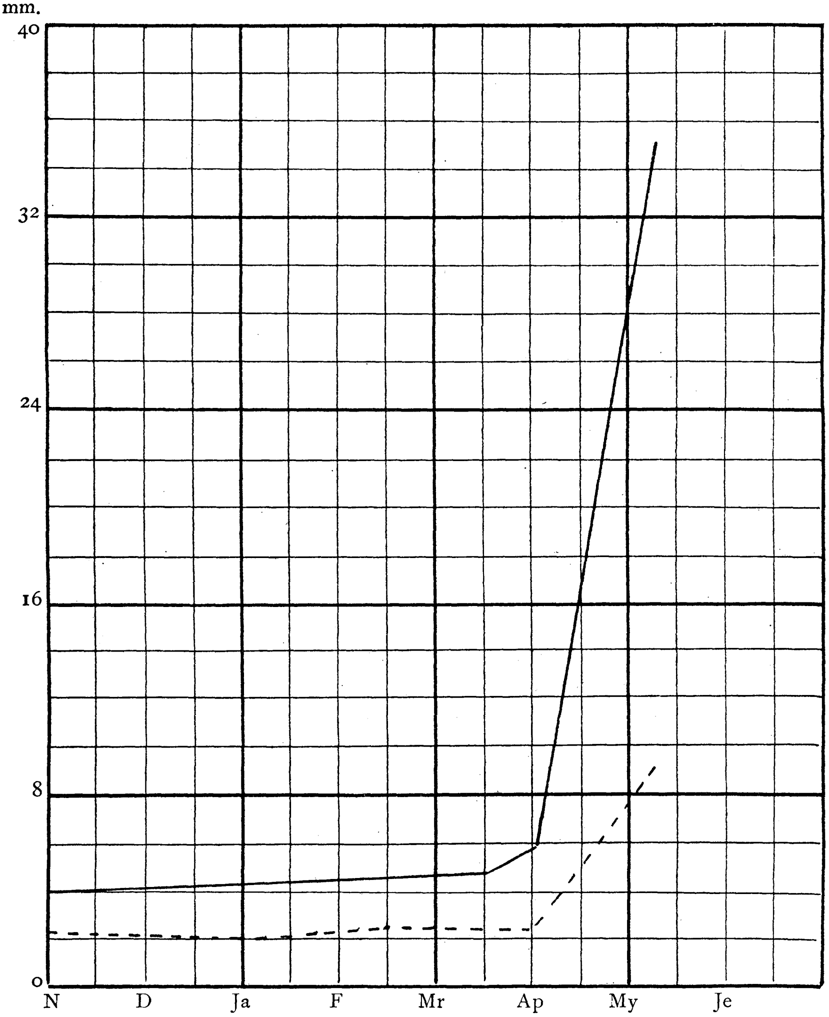

FIGURE A. *Ulmus americana*. Curves of growth of the buds in length and diameter.

season. However, the sudden growth of the leaves, as though pushed out *en masse*, indicates that there are no new additions. The organization of a terminal bud and axillary buds as soon as the leaves unfold tends to substantiate this view.

In a consideration of the number of leaves in the buds of *Quercus alba* neither the gross nor the microscopic study was entirely satisfactory. The leaves are not only exceedingly minute but they are densely covered with hairs which render sectioning difficult. Complete sections were too few to be of value in determining the actual number of leaves in the bud, but the unbroken vegetative points were more often secured and their study would indicate an approach, at least, to the full number of leaves. This

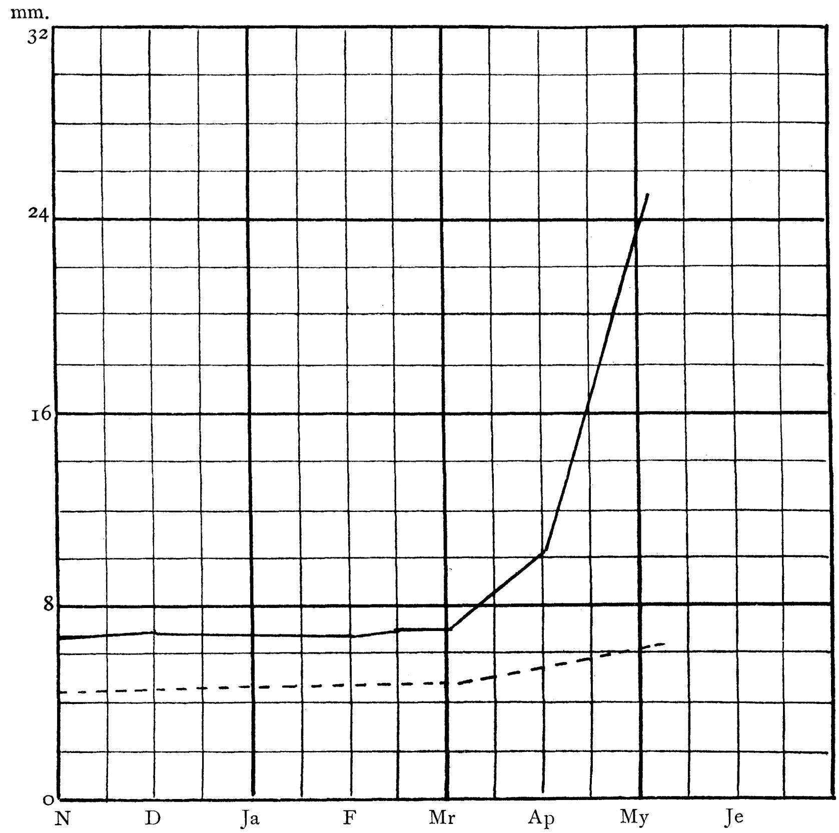

FIGURE B. *Syringa vulgaris*. Curves of growth of the buds in length and diameter.

is especially true of buds which show in section numerous scale-like growths around the meristematic point. These scale-like growths appear, in the unfolding bud, to be the stipules of the whorl of leaves at the distal end of the young stem (FIGURE 48). Since the whorl is not a true one but is produced by a shortening of the internodes in this part of the stem, the number of leaves at the beginning of winter for this species is still a matter of conjecture. Buds of *Quercus rubra* give stronger evidence of containing the complete number of leaves in that the leaves with the new terminal bud and the whorl of axillary buds are pushed out and developed simultaneously, as in *Populus*.

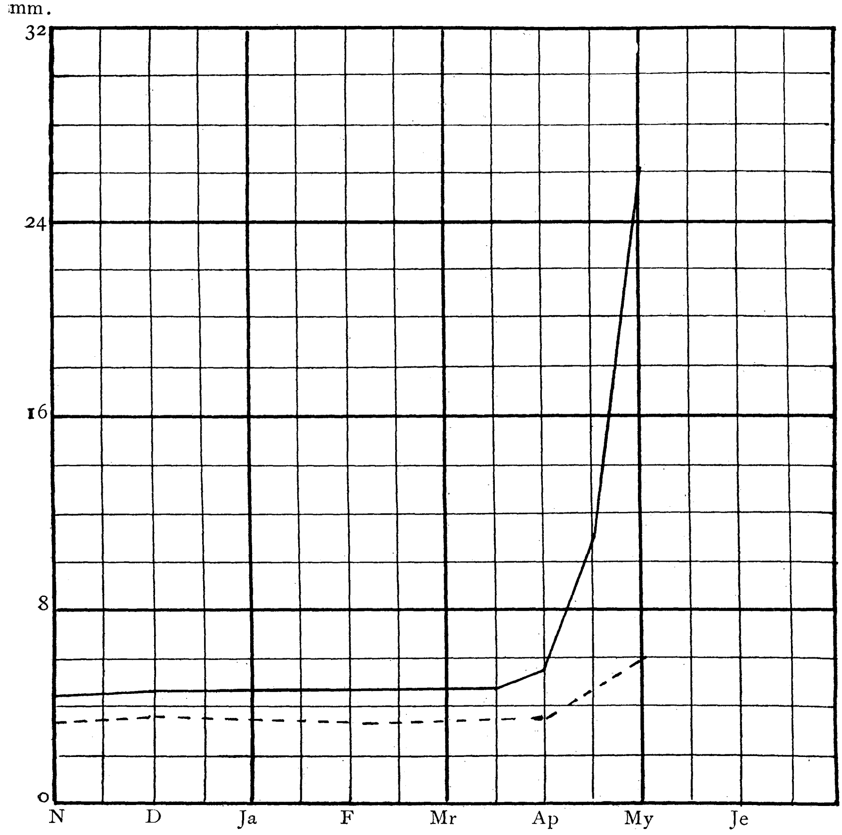

FIGURE C. *Quercus rubra*. Curves of growth of the buds in length and diameter.

From evidence accumulated from November, 1905, to May 22, 1906, it is probable that in *Betula populifolia* the full number of leaves, five to eight in terms of nodes, does not exist in the bud during the winter. Two well-formed leaves are readily distinguished, but the rest of the bud is a gelatinous mass from which only one or two leaf-like bodies can be extricated. When the bud unfolds, the two well-formed leaves expand at once but the rest of the bud undergoes an exceedingly slow development, during which period it is probable that new additions of leaves are made.

In *Ulmus americana*, in *Tilia vulgaris*, and in *Alnus incana*, the leaf content cannot be determined with any reasonable degree of accuracy beyond the fact that a large proportion if not all of the leaves which unfold are present during the winter. The irregularity in the number of leaves and nodes renders a comparison of these quantities valueless. The answer to this question, as in the other doubtful cases, must be sought in a microscopic study of the development of the buds from the beginning of the swelling period in April and May to the end of leaf expansion in summer.

To summarize briefly, the full number of leaves which unfold in the spring exists in the winter buds of *Acer platanoides*, *Aesculus Hippocastanum*, *Fagus americana*, *Fagus sylvatica*, *Fraxinus americana*, *Liriodendron Tulipifera*, *Hicoria ovata*, *Philadelphus*, *Picea excelsa*, and *Populus tremuloides*. In *Syringa vulgaris* the full number may or may not exist. In the last case, the number probably developed in the spring does not exceed one or two pairs of leaves, which soon die when the meristematic point ceases to function. Although the number of leaves in the bud approaches the number characteristic of this species there still remains an element of doubt in the following: *Rhododendron maximum*, *Quercus alba*, *Ulmus americana*, *Tilia vulgaris*, and *Alnus incana*. New additions of leaves probably take place in *Betula populifolia*, in *Salix fragilis*, and in *Salix alba*.

Measurements of buds : It is a striking coincidence that those winters during which observations on the size of the bud have been carried on have been winters of extraordinary mildness.

Askenasy (1877), whose investigations on the growth of the flower buds of cherry extend over a period of three years, says: "It is an important fact that greater warmth in winter exercises but little influence on the growth of cherry buds. However, when

Cornus mas and *Forsythia viridissima* bloom in early January, as they often do, it is possible that the temperature of the fall and winter months has a higher significance for these species than for cherry."

Küster (1899) holds that those organs in which growth is demonstrable during an unusually mild winter cannot fail to show some advance in a normally cold one.

Buds which were measured during each month of the winter 1905–6, show no appreciable increase in length or in diameter, although the winter was one of unusual mildness, a winter in which the mean temperature, 27° F. for the coldest month, was exceedingly high. The buds of the following species appeared absolutely dormant: *Fagus americana*, *Fagus sylvatica*, *Quercus alba*, *Quercus rubra*, *Tilia vulgaris*, *Tilia americana*, *Hicoria ovata*, *Hicoria microcarpa*, and *Fraxinus americana*. The flower buds of *Alnus incana*, *Ulmus americana*, *Betula populifolia*, *Populus tremuloides*, *Salix fragilis*, and *Salix alba* are more or less easily influenced by continuous high temperatures and consequently

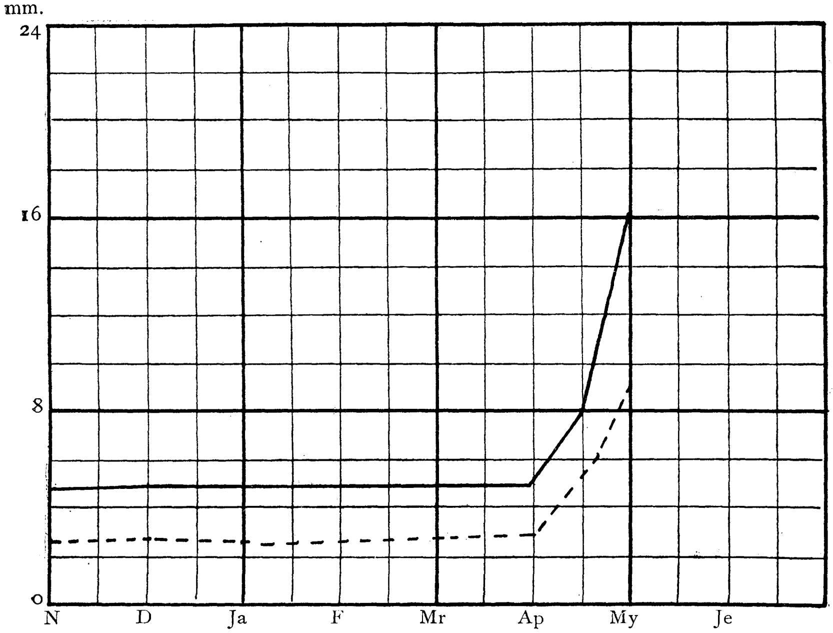

FIGURE D. *Quercus alba*. Curves of growth of the buds in length and diameter.

show a variable development. The flower buds of *Ulmus* and the catkins of *Alnus* were noticeably larger in January. In some cases the catkins of *Salix* and *Populus* had pushed aside their scaly coverings as early as December, but such precocious growth in these two genera is confined to the flower buds of saplings and of immature growths. Favorable situations and exposure to warm sunshine are apparently factors which influence such premature development.

Sendtner (1851) observed that different parts of a plant show a different attitude toward the varied influences and growth stimulations affecting them during the winter months.

According to Schimper (1903), it has been proved experimentally that the flower buds, or reproductive organs, possess a lower optimum temperature for growth than is the case with leaf buds, or vegetative organs. This principle is apparent in nature, since, in each species observed during the winter of 1905–6, the true leaf bud is in all respects less active than the flower bud.

Wiegand (1905) mentions the fact that flower buds do not increase in size until late spring. Similarly, the leaf buds of the trees and shrubs studied in this investigation show practically no increase in size during the winter rest-period. At least their normal condition of apparent rest is not disturbed in so far as their external appearance is concerned.

The curves of growth (figures *A–J*) indicate a slight alternating increase and decrease during the winter, a gradual increase during March and a more rapid advance in April. The fluctuations of the curve during the winter months are a result of difficulties encountered in measuring the buds. The outer scales often dry out and many either loosen or fall away. This is clearly the case in *Hicoria*, *Picea*, and *Alnus*. The quantity and consistency of scale varnish varies also. But in spite of these difficulties a gradual continuous growth, if present, could not fail to be observed and recorded in a series of measurements which are made at regular and frequent intervals during the winter and spring. The curves of growth are therefore of value in illustrating the time and rapidity of swelling, as well as the variations which are exhibited by the different genera and species.

The time at which the different plants under investigation

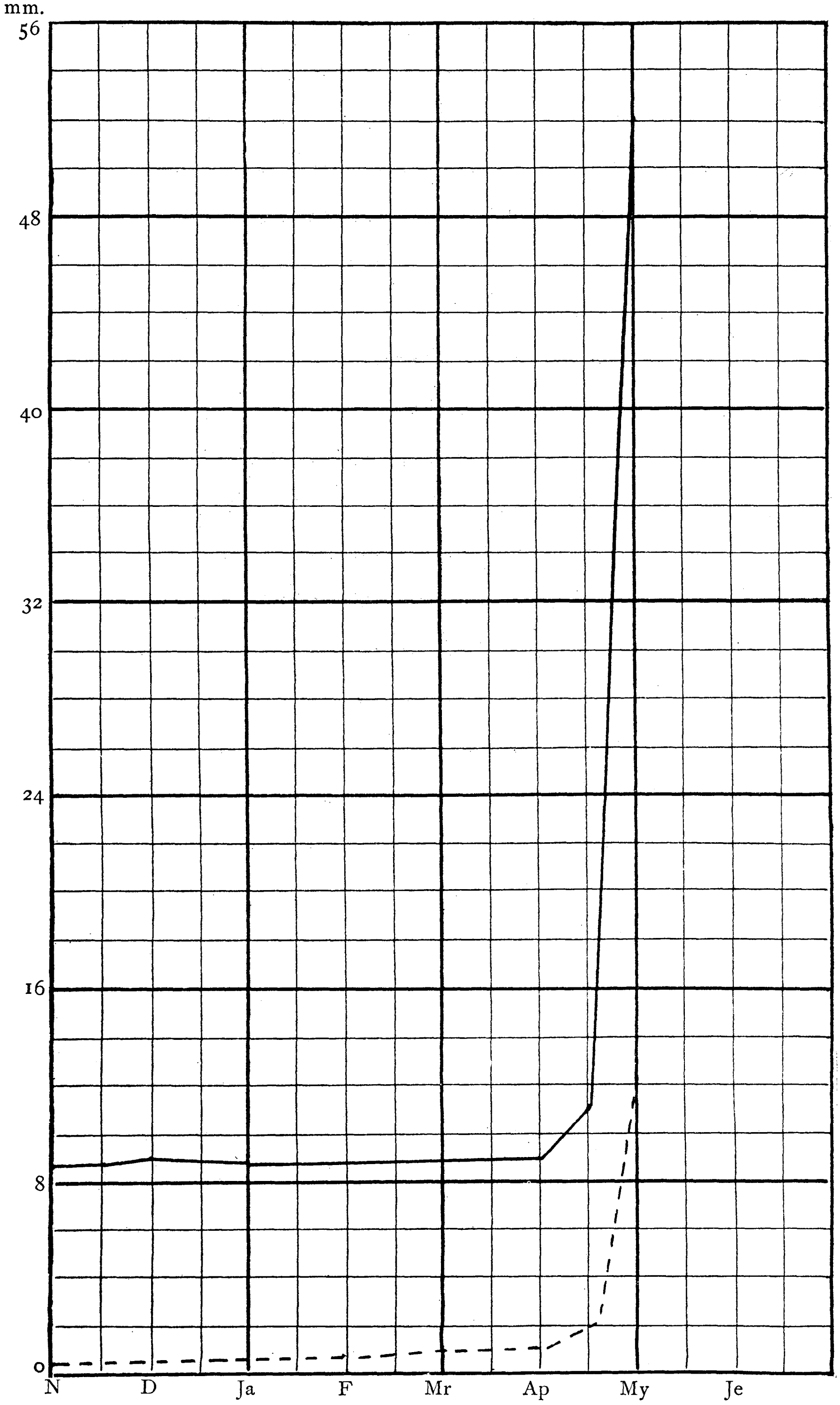

FIGURE E. *Hicoria ovata*. Curves of growth of the buds in length and diameter.

renew their growth in the spring varies considerably, as will be seen from the following curves. The curve of *Ulmus americana* illustrates a retardation in growth of about two weeks beyond that of *Syringa vulgaris* (FIGURES *A*, *B*). *Quercus rubra* and *Quercus alba* vary somewhat (FIGURES *C*, *D*). The buds of the two species of *Hicoria* differ not so much in time as in rapidity of development (FIGURES *E*, *F*). A greater delay in the swelling and unfolding of the buds occurs in *Tilia* and in *Betula* (FIGURES *G*, *H*). Buds of the two evergreens, *Rhododendron* and *Picea*, remain in a state of apparent rest until a later date than the buds of any other species that have been studied (FIGURES *I*, *J*).

Henslow (1901) remarks: "Buds are primarily the result of the lowering of temperature in autumn; for as soon as this rises above a certain degree they burst open and begin to grow." A comparison of the curve of temperature with the curves of growth indicates that temperature is not the only factor controlling the growth of buds. It will be seen that growth took place in March at a lower temperature than in the preceding winter months. Zero temperatures appear to have no effect on the size of the bud. Buds both with dry and with somewhat succulent scales were measured with the thermometer at 0° F. No difference in size could be detected as a result of these measurements. Wiegand (1905) records a similar observation for buds but finds a decided contraction in twigs due to the expulsion of air from the intercellular spaces.

As a rule, the first apparent evidence of growth in the bud is in the appearance, at the distal end, of small tufts lighter in color than the outer scales. These tufts were the elongating inner scales, which were soon followed by the leaves themselves. The increase in the diameter of the buds was proportionally much slower than the increase in length. A comparison of the field observations with the microscopic sections of the buds gives evidence of growth within the bud before it becomes visible externally. This was most clearly apparent in *Aesculus* (FIGURE 38).

Such observations regarding the period of rest and growth in buds may come to the eye of any careful and painstaking observer in the field. What takes place within the scales during this time is not so easily observed, yet one must admit that the unfolding of the leaf is only the last phase of a long-continued development whose stages of progress can be little known without a microscopic study of the internal structures and tissues.

MICROSCOPIC STUDY OF GROWTH

It is not the purpose of this investigation to trace the growth and development of leaves or leaf tissues from a purely embryological or cytological standpoint, but to consider changes in the size of cells already present, the addition of new cells or tissues, and the organization of new leaf fundaments.

A microscopic study of buds taken from the somewhat miscellaneous collection of trees and shrubs previously mentioned reveals a wide variability in the stage of development at which the leaf buds enter the winter rest. At one extreme stand *Fagus americana* and *Fagus sylvatica* with all of their leaves well formed and the future terminal and axillary buds present and in an advanced stage of development. At the other extreme stand *Betula*

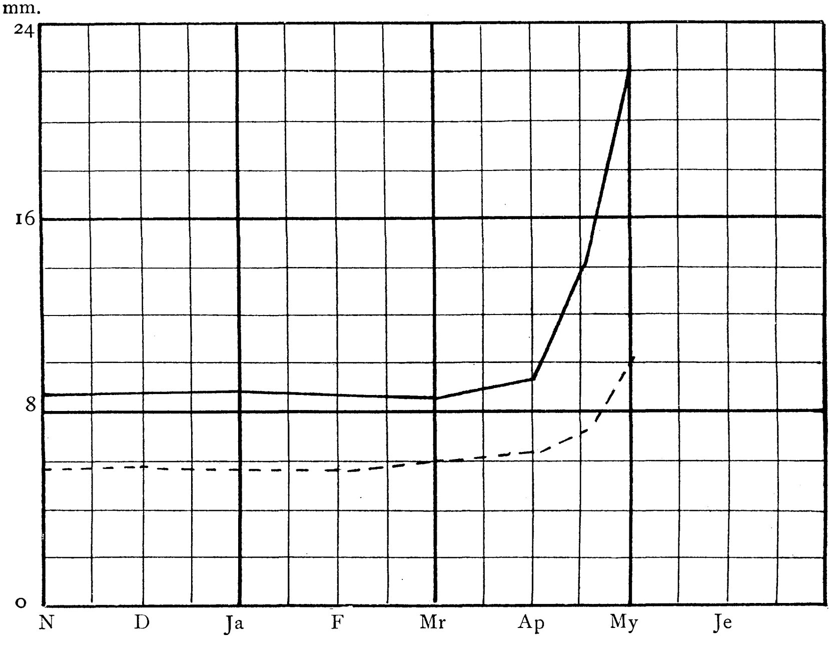

FIGURE F. *Hicoria microcarpa*. Curves of growth of the buds in length and diameter.

populifolia, *Salix fragilis*, and *Salix alba*, with an incomplete number of leaves and the axillary buds absent.

In *Fagus* neither the axis nor the axillary buds (FIGURE 15) show any change whatsoever until the April swelling which precedes the unfolding of the bud. Other cases in which the axillary buds are present in rudimentary form during the winter are *Fraxinus americana* (FIGURES 34 and 35), *Quercus alba* (FIGURES 46 and 47), *Ulmus americana* (FIGURES 17 and 18), *Alnus incana* (FIGURE 51), and *Syringa vulgaris* (FIGURE 8).

Mere areas of cells, which are rich in protoplasm and are stained more deeply than the surrounding tissue, occur in the leaf axils of *Liriodendron Tulipifera*, *Salix fragilis*, *Salix alba*, and *Acer platanoides*. No indications of axillary buds appear in the following: *Aesculus Hippocastanum*, *Picea excelsa*, *Rhododendron maximum*, *Tilia vulgaris*, *Populus tremuloides*, *Betula populifolia*, and *Philadelphus*.

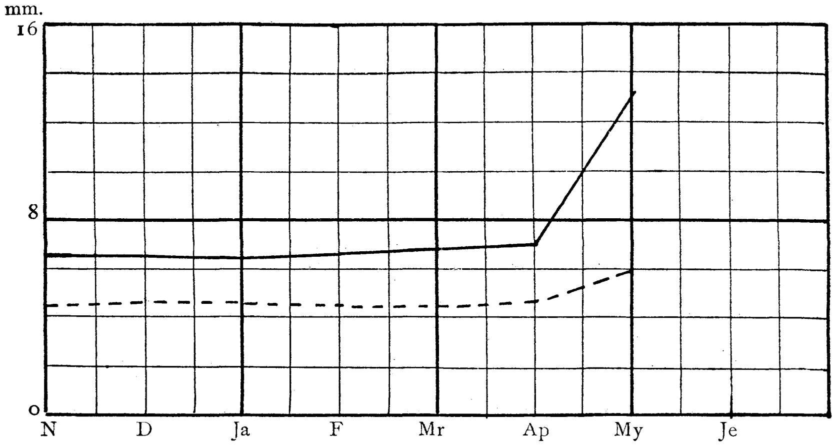

FIGURE G. *Tilia vulgaris*. Curves of growth of the buds in length and diameter.

In the flower bud, according to Coulter and Chamberlain (1903), the spore-mother-cell stage seems to be the usual halting place at the beginning of the rest period.

In an embryological study of *Ulmus americana*, Shattuck (1905) found the cells within microsporangia in the mother-cell stage in the early part of February and assumed that they passed the winter in this stage.

Miss Ferguson (1904) found in *Pinus* that the archesporial tissue was not differentiated into the spore-mother-cells until April, thus disproving Coulter and Chamberlain's general statement, as well as their special one, in regard to the gymnosperms.

Chamberlain (1898) says: "The flower buds of *Salix* pass the winter in the pollen-mother-cell stage." This general statement for *Salix* is questioned since flower buds of *Salix fragilis* gathered in November did not follow this rule. In this case the cells of the anther appear to be homogeneous and show no differentiation of tissues.

It follows from these different observations that both leaf buds and flower buds enter the winter in various stages of development. The exact point at which growth is suspended appears to be an inherited characteristic rather than one solely dependent upon climatic conditions.

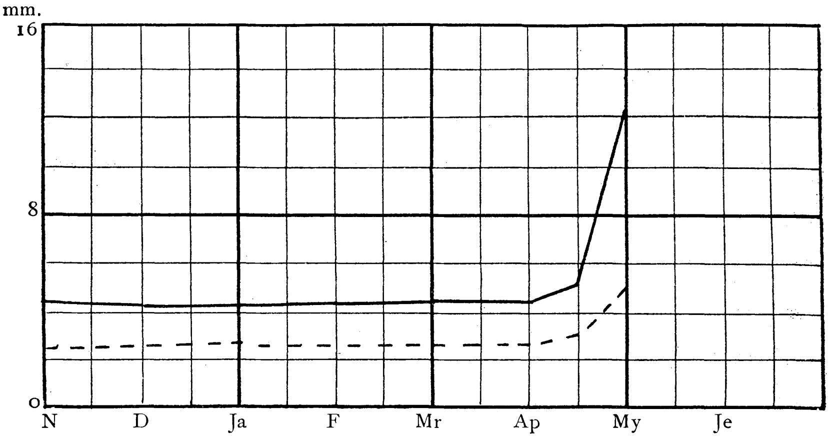

FIGURE H. *Betula populifolia.* Curves of growth of the buds in length and diameter.

We have seen that most buds, as a rule, do not increase appreciably in size during the winter months. The question that naturally arises is: Are these buds absolutely quiescent from November to February or are they undergoing changes which are not apparent externally?

Pfeffer (1903) claims that the influence of the continued cold of winter seems to have produced in the life of most plants in the colder zones a well marked period of rest. Strasburger (1903) says: "It is not in reality an absolute rest; for although the outwardly visible processes of development and growth stand still, the internal vital processes, although retarded, never altogether cease."

The investigations of Miyaké (1902) demonstrate that in evergreen leaves "starch is formed by photosynthesis in winter, though feebly, and its translocation occurs in the same season."

According to Fischer (1891), who has made many important observations on the metabolic processes which occur within the tree during winter, various activities and movements of the reserve material take place in the interior of the tree long before any externally visible changes become apparent. The starch which is stored in the pith of the young shoot moves toward the buds and accumulates in the embryonic leaves and flowers from which hitherto it has been absent. It is a reserve material and just suffices for the first stages of growth preceding the swelling of the buds.

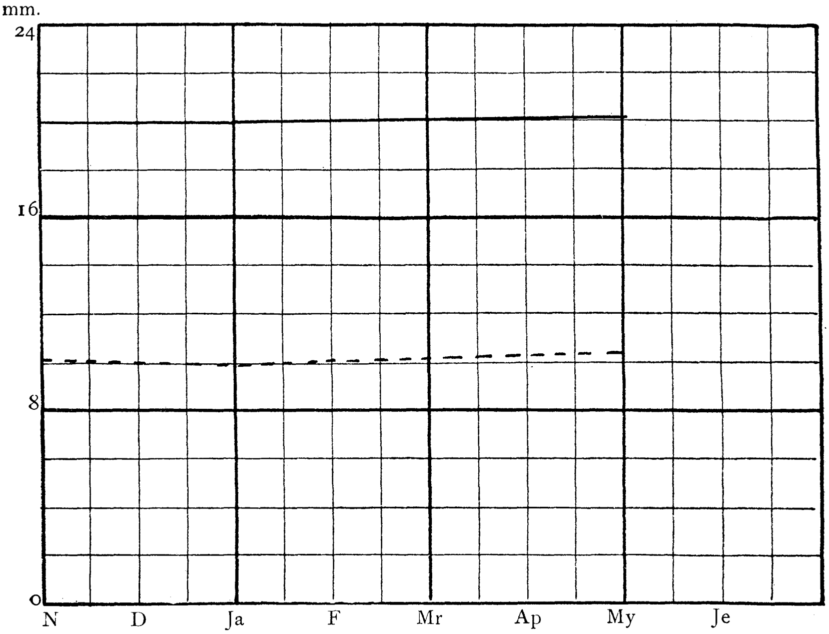

FIGURE I. *Rhododendron maximum.* Curves of growth of the buds in length and diameter.

Hartig (1861) observed that the duration of time during which this transportation of reserve food takes place is about the same for all trees, two months in all, but that the beginning of this activity varies in different trees. Activity begins about the middle of February in *Acer*, and about the middle of March in *Quercus*.

Baranetzky (1873) suggests that the power of bleeding, which is so frequently observed in plants, is a direct expression of the internal changes which are repeated every year in hibernating trees.

Halsted (1890) observed in February small quantities of starch in the pistil and in the filaments of stamens, organs which in early winter do not contain this reserve food.

It is possible that as a result of these metabolic processes growth is induced, although ever so slowly, and serves as a preparation for the sudden and rapid development of the young leaves and embryonic parts of the bud in the spring.

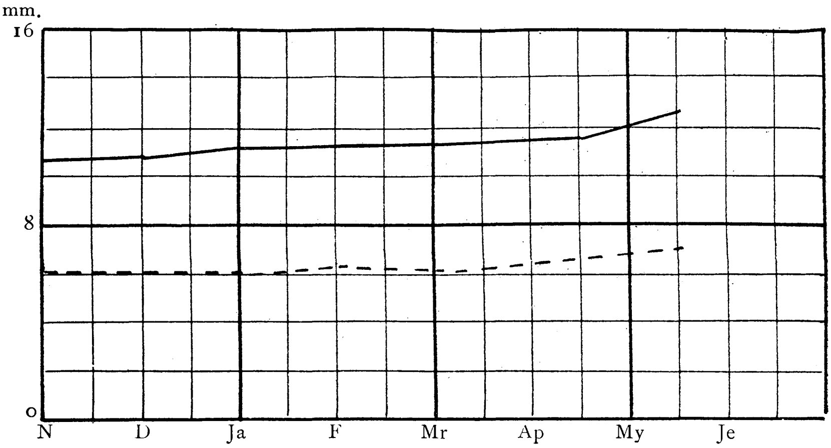

FIGURE J. *Picea excelsa.* Curves of growth of the buds in length and diameter.

There are many difficulties necessarily in the way of determining absolutely any increase due to the stretching of cells in the leaf or in the leaf fundaments of the bud. In comparing buds for the different months of the rest period, slight variations in size and in stage of development must be expected, but irregularities in this respect are minimized by a comparison of a large number of similar buds.

The median sections of buds and meristematic points illustrated in the present investigation were drawn after a comparative study of more than a thousand slides of serial sections representing over five hundred buds. It will be seen by reference to the plates that the leaf fundaments or lobes of homogeneous tissue, and the young leaves, which increase in size and in degree of development toward the periphery of the bud, are arranged in acropetal order around the meristematic point (FIGURES 1, 8, 30).

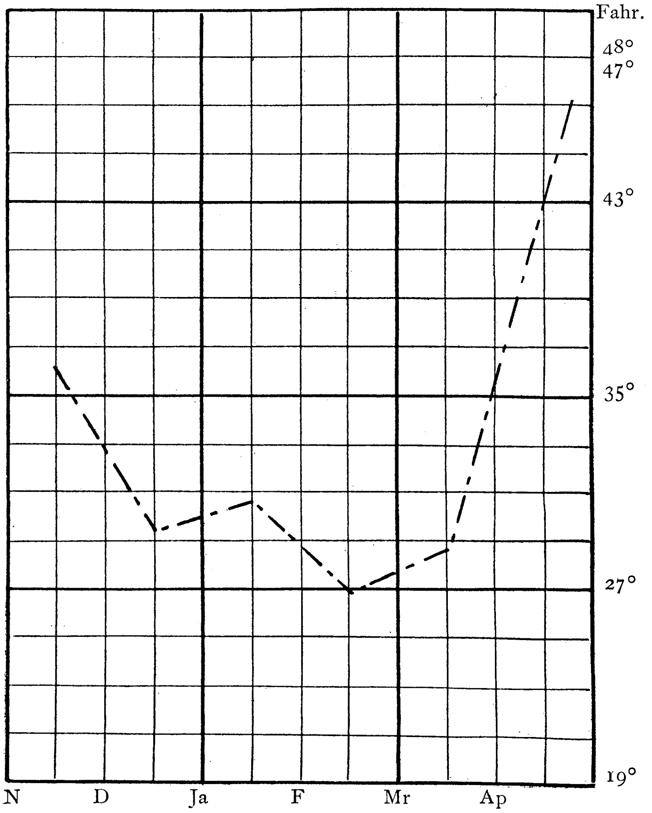

FIGURE K. Temperature curve.

In the species under investigation, growth of the leaf bud by addition of new tissue does not take place during November, December, or January. It seems apparent, however, that a stretching of cells occurs in many instances and manifests itself in the greater convexity of the meristematic point and its consequently crowded condition (FIGURES 3, 4, 9, 21, 22). This stretching in the apical part of the meristematic region causes no change in the size or in the external appearance of the buds under investigation, although it becomes a measurable factor in the leaf buds of *Sambucus* and of *Prunus*, species which more readily respond to the continuous high temperatures of an unusually mild winter.

Küster says that during the warm winter of 1899 leaf buds of *Acer platanoides* showed not only a stretching of the cells but also an addition of new tissue in the axils of the upper leaves. These results must be seriously questioned, for his drawings of free-hand sections do not give the accuracy of detail which the microtome sections reveal. A careful search through many series of sections proves conclusively that what Küster called new tissues are the basal parts of the petioles which partially encircle the young axis of the bud (FIGURES 31 and 32).

All cells in the tissues of the winter buds are exceedingly small and closely packed together. A pronounced stretching of the tissue occurs in the following species during February: the inner scale fundaments of *Aesculus Hippocastanum* increase in length (FIGURE 38); the rudimentary leaves of *Syringa vulgaris* appear larger (FIGURE 10); the bud of *Philadelphus*, which in its dormant state is buried beneath the leaf scar, protrudes as a tiny bud through the rift in the upper portion of the scar.

The mean temperature for the month of March was exceptionally low for that month (FIGURE K), yet there are many evidences that growth occurred. *Liriodendron* and *Acer* show minute cushions of tissue which later develop into axillary buds (FIGURES 5 and 32). In *Alnus* the cushions of tissue increase slightly in size (FIGURE 51). A change in the color of the *Salix* buds, a change from a dull red to a more living one, gives evidence that the life processes are more active; their interior structure also reveals growth by the enlargement of parts at the growing tip (FIGURE 23), and in the more deeply staining tissue at the leaf axils. Buds of *Fraxinus* show no additional tissue but a general stretching of all parts. These buds which show a gradual but unmistakable advance in interior structure through February and March undergo rapid and vigorous growth in April when the leaf blades become more or less expanded and free.

In leaf buds which develop more slowly, as in *Quercus*, *Hicoria*, *Fagus*, *Populus*, and *Tilia*, there is little evidence of growth or stretching in the meristematic points or other local areas from November to March inclusive. It seems probable that growth entirely, or almost entirely, ceases for a time. A cytological and a physiological study of these parts as they occur during the winter is required to verify this conclusion.

Geleznoff (1851), a Russian investigator who studied the leaf buds of *Quercus* and *Betula* in their winter condition, says: "All buds make some advance in growth of new tissues and organs from December to February even at continued temperatures of 0° and less." It is possible this report of the organization of new parts at such temperatures is the result of incorrect observations of unlike buds, for plant physiologists hold that the growth and the construction of new organs at temperatures below 0° is impossible (Davenport, 1897).

In late March and early April the buds of *Quercus*, *Hicoria*, and *Fagus* begin a general swelling which becomes noticeable in a lengthening of the internodes and a more crowded condition of the meristematic point. *Betula*, *Populus*, and *Tilia* remain dormant for a longer time. Sections of the last two species indicate changes by the 16th of April in the general length of scale or leaf fundaments, and irregularities in the outline of the meristematic surface (FIGURES 26 and 29). Aside from the stretching of cells, the outline of the buds of *Betula* remains the same, but in the region of the leaf axils the tissue becomes more deeply staining than heretofore. On April 16 the leaf buds of *Picea* and *Rhododendron* appear as in the preceding months of the rest period (FIGURES 40–43). Observations on *Picea* in early May reveal an alteration in the papilla-like leaves which from now on assume rapidly their needle-shaped character. No change, up to this time, is visible in the leaf buds of *Rhododendron*.

SUMMARY

In some species the full number of leaves that unfold in the spring exists at the beginning of winter. In other species, the majority of leaves are present at this time and additions occur at the time of unfolding. The terminal and axillary buds of the next summer and autumn are in many cases well organized at the approach of winter.

The leaf buds of all deciduous and evergreen trees and shrubs investigated enter upon a winter resting period, the duration of which varies in the different plants.

The greater warmth of an unusually mild winter exercises but little influence on the growth of leaf buds. Flower buds respond more quickly to the influence of continuous high temperatures.

Of the species under investigation, some leaf buds show no change either in length or in diameter until February or March; others not until April or May.

In some cases growth may take place in February and March at lower temperatures than prevail during the preceding winter months.

Organization of additional tissues does not take place within the leaf buds during the winter but becomes apparent in March or April. A stretching of cells occurs in the meristematic region of some species as early as December and January, and manifests itself by a greater convexity of the meristematic surface. This change is microscopic and produces no change in the external appearance of the buds.

The first apparent evidence of growth is a swelling of the closely compacted tissues. With continuous high temperatures rapid and vigorous growth follows.

The leaf buds of the two evergreens investigated, *Picea* and *Rhododendron*, exhibit the longest rest period.

For valuable aid and supervision in carrying on this investigation most grateful acknowledgment is given to Dr. Margaret C. Ferguson, of Wellesley College.

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Explanation of text figures and of plates 9-11

Figures *A–J* represent the curves of growth of the buds in length and in diameter. Figure *K* is the temperature curve. The continuous line indicates growth in length. The dotted line indicates growth in diameter. The dot and dash line shows the mean temperature. The numerals on the axis at the left of curves *A–J* represent the growth of the bud in millimeters. The numerals at the right of curve *K* indicate the mean temperatures, Fahrenheit. The bottom line represents the time during which measurements were made, the 25th of November, December, and January, the 10th and 25th of February, March, April, and May. As a rule, for each species, the measurements of ten buds are averaged for each curve. The curves end at the time of unfolding of the bud.

All figures in plates 9–11 were drawn with the aid of the Abbé camera lucida. A Zeiss microscope was used. All figures represent longitudinal sections. Figures 1 and 8 are magnified 10 times; all others are magnified 25 times. The abbreviations used in the explanation of plates are as follows:

Axis of incipient shoot, *a.*; axillary bud, *ax.b.*; base of petiole, *b.p.*; leaf, *l.*; leaf fundament, *l.f.*; petiole, *p.*; scaly covering, *s.c.*; scale fundament, *s.f.*; stipule, *st.*; terminal bud, *t.b.*; vegetative point, *v.p.*; vascular tissue, *v.t.*

PLATE 9

1–6. *Liriodendron Tulipifera*

1. Median longitudinal section of bud with two outer leaves removed. November.

2. Vegetative point during rest period. 29 D.

3, 4. Greater convexity of vegetative point and crowding of parts. 30 Ja, 28 F.

5. A general elongation of axis, of leaf, and of scale fundaments. 30 Mr.

6. Bud two weeks later than in preceding figure. Marked increase in size. 16 Ap.

7–14. *Syringa vulgaris*

7. Appearance of vegetative point during winter rest period. 25 N.

8. Median longitudinal section showing appearance of axis during winter. January.

9. Appearance of vegetative point in winter. 30 Ja.

10. Elongation of leaf fundaments. 28 F.

11. Stretching of parts and addition of upper axillary buds. 30 Mr.

12, 13. Two stages of vegetative point on April 16.

14. Axillary bud. 5 My.

15 and 16. *Fagus americana*

15. Typical structure of an axillary bud as found within the terminal bud during winter. November, March.

16. Same, showing increase in size. 16 Ap.

17–19. *Ulmus americana*

17. General appearance of vegetative point during winter. November.

18. Greater convexity of vegetative point. 30 Ja.

19. General growth of meristematic region. 16 Ap.

20–24. *Salix fragilis*

20. Winter condition of vegetative point. November, December.

21, 22. Greater convexity of vegetative point. 30 Ja, 28 F.

23. General stretching of meristematic region. 30 Mr.

24. Additional growth of new organs. 16 Ap.

25 and 26. *Tilia vulgaris*

25. Winter condition of vegetative point. February.

26. Greater breadth at vegetative point. March.

27. *Betula populifolia*

Appearance of apical part of bud in winter and spring. November, April.

28 and 29. *Populus tremuloides*

28. Winter condition of apical region. November, March.

29. General stretching and growth of meristematic region. 16 Ap.

PLATE 10.

30–33. *Acer platanoides*

30. Appearance during rest period. November, December.

31. General stretching of parts in meristematic region. January, February.

32. Appearance of scale fundament and upper axillary bud. 30 Mr.

33. General growth of parts and appearance of future terminal bud. 16 Ap.

34 and 35. *Fraxinus americana*

Appearances during rest period and early spring. November, March.

36–39. *Aesculus Hippocastanum*

36, 37. Appearances during rest period. November, January.
38. Elongation of scale fundaments. 28 F.
39. Broadening of apical region. 30 Mr.

PLATE 11

40 and 41. *Picea excelsa*

General dormant condition during winter and early spring. November, March.

42 and 43. *Rhododendron maximum*

Dormant condition during winter and spring. November, 16 Ap.

44 and 45. *Philadelphus*

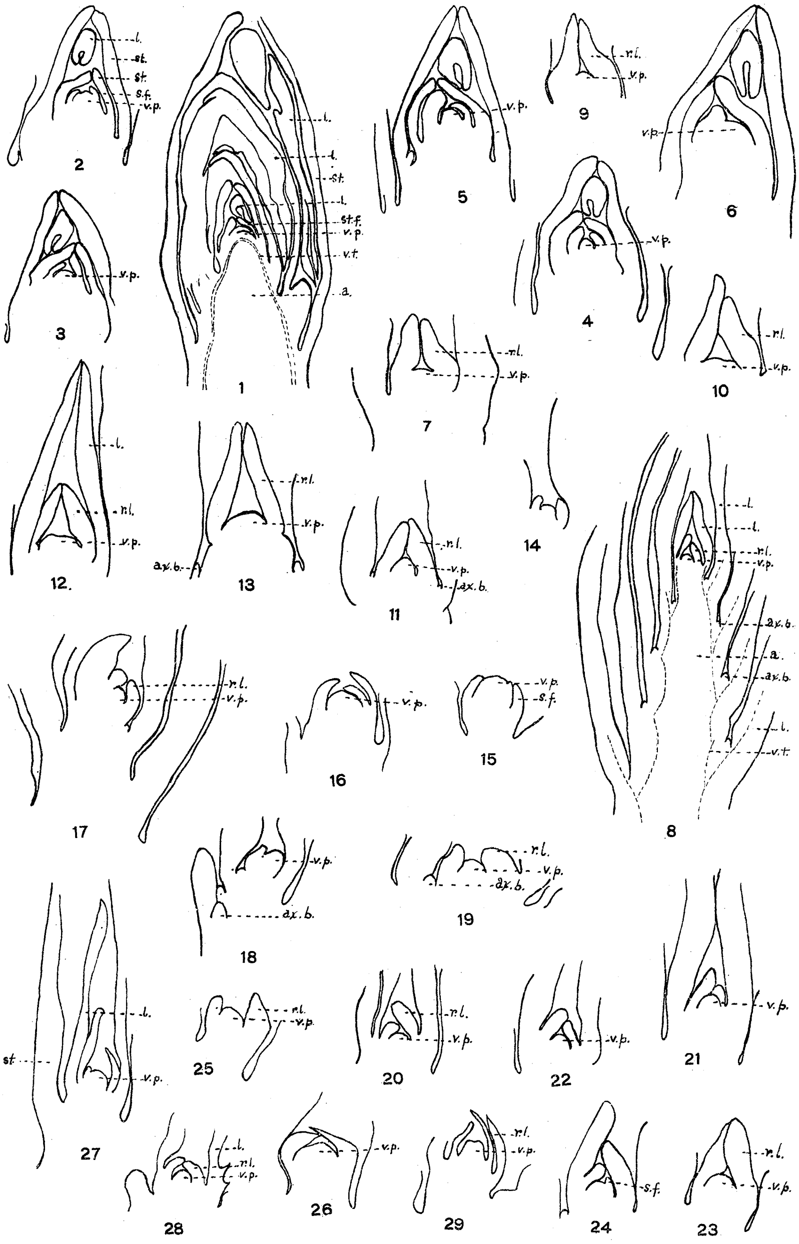
44. Median longitudinal section of bud, showing winter condition. November, January.
45. Median longitudinal section of bud, showing stretching of parts. February, March.

46–48. *Quercus alba*

46. Axillary bud within the terminal bud at beginning of rest period. November.
47. Winter condition of vegetative point. December, March.
48. General stretching of parts. 16 Ap.

49–51. *Alnus incana*

49, 50. Appearances during winter rest period. November, February.
51. General growth in apical part of meristematic region. 30 Mr.



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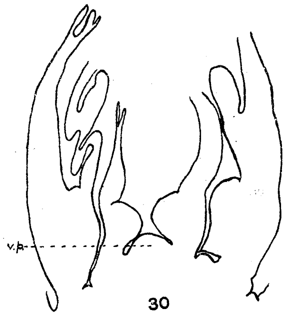

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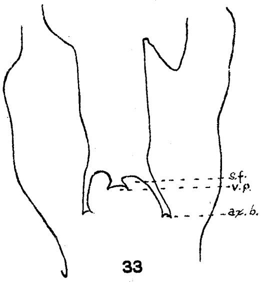

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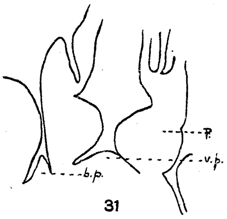

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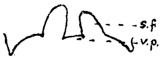

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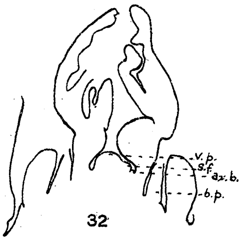

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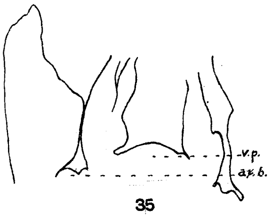

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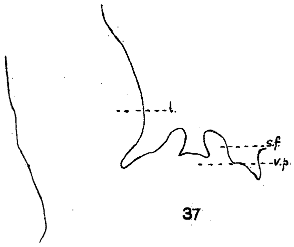

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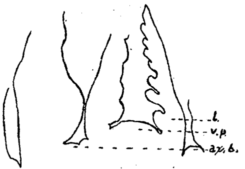

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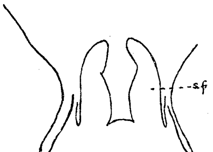

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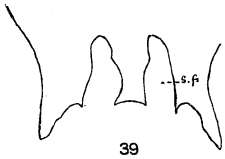

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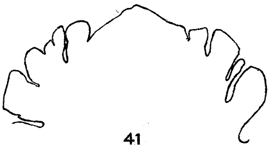
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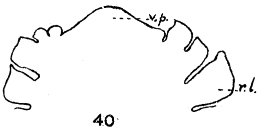

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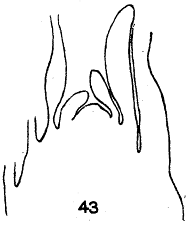
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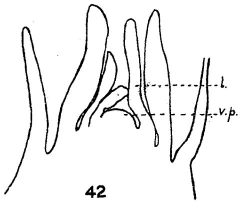

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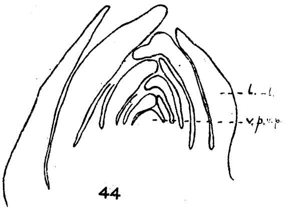

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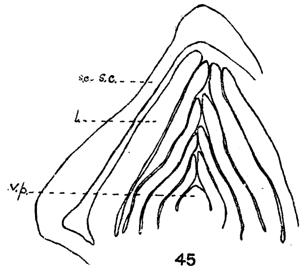

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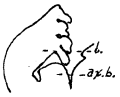

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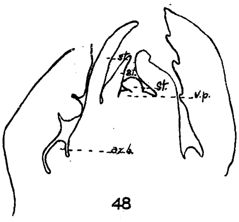

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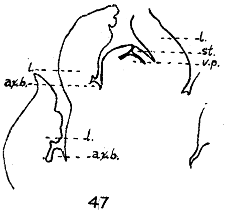

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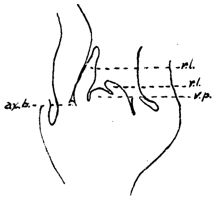

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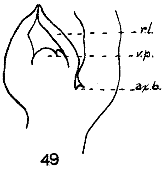

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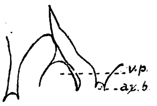

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